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You can run, but you will never escape: A new species of *Psyllaephagus* Ashmead (Hymenoptera, Encyrtidae), parasitoid of the classical biological control agent *Boreioglycaspis melaleucae* (Moore) (Hemiptera, Aphalaridae) in Florida, USA

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Abstract

Melaleuca quinquenervia (Cav.) S.T. Blake (Myrtales: Myrtaceae) is an invasive tree in Florida, USA, for which a psyllid, *Boreioglycaspis melaleucae* (Moore) (Hemiptera: Aphalaridae), was successfully established in April, 2002 to control its spread. A parasitoid wasp, *Psyllaephagus migrator* McClelland, **sp. nov.** was found to parasitize this psyllid in Australia, which we consider to be its native range, and in Florida, where we consider it to be adventive. We provide a description, high resolution images and morphological diagnosis for *P. migrator* and a molecular data set of five gene regions to facilitate its identification and use in phylogenetic studies. The biology of the parasitoid is presented with documentation of its immature stages. Trapping data suggest that *P. migrator* has reduced populations of the biocontrol agent *B. melaleucae* in Florida.

Keywords
Biocontrol, *Melaleuca quinquenervia*, taxonomy, Tri-trophic

Introduction

Melaleuca quinquenervia (Cav.) S.T. Blake (Myrtales: Myrtaceae) is an invasive tree of major economic and environmental impact in the subtropical wetland Everglades ecosystem of southern Florida. Resistant to management by cutting and burning, *M. quinquenervia* has been the target of a multi-decade, multi-organism classical biological control program utilizing the weevil *Oxyops vitiosa* (Pascoe) (Coleoptera: Curculionidae), two species of *Lophodiplosis* Gagné (Diptera: Cecidomyiidae), and the psyllid *Boreioglycaspis melaleucae* (Moore) (Hemiptera: Aphalaridae) (Center et al. 2000, 2006; USDA 2008; Smith et al. 2020; Smith 2022) (Fig. 1). This suite of classical biological agents is touted as a great success in Florida, having achieved conditions for sustained maintenance-control of *M. quinquenervia* in areas where the tree once thrived in near monoculture (Center et al. 2008, 2012; Rodgers 2016). The initial release of *B. melaleucae* occurred in April 2002 in Broward County, FL. Material was introduced from Australia under permit (FSCA# 1997-3413) (Halbert and Burckhardt 2020). Voucher specimens for the permit and for the insects used in the official first release are deposited in the Florida State Collection of Arthropods (FSCA) housed at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry (FDACS-DPI, Gainesville, FL, USA).

In 2020, an unidentified species of *Psyllaephagus* Ashmead (Hymenoptera: Encyrtidae) was reared from wild populations of *B. melaleucae* in Palm Beach County, Florida. The same wasp was collected again in 2021, 2022, and 2023, having emerged from *B. melaleucae* in St. Lucie County, Florida (Fig. 2). This *Psyllaephagus* species has apparently established populations in Florida. Whether the species represents a previously undetected native wasp or a recent introduction seemed nearly impossible to determine given the state of research on the genus. *Psyllaephagus* are exceedingly difficult to identify due to a lack of comprehensive revisionary works on the genus, chronic taxonomic neglect in biogeographic regions where the genus is hyper-diverse, lack of DNA sequence data for comparison, and the poor quality of legacy biodiversity literature that treated *Psyllaephagus* from Australia.

Examination of specimens in the Florida State Collection of Arthropods (FSCA), Florida Department of Agriculture and Consumer Services, Division of Plant Industry (FDACS-DPI), Gainesville, Florida, allowed for an initial comparison of the unidentified species to *P. yaseeni* Noyes and several other undetermined *Psyllaephagus*, yielding no morphological matches. Further consultation with the few available *Psyllaephagus* experts led to the conclusion that the *Psyllaephagus* reared from *B. melaleucae* in Florida was best treated as an undescribed species. In this contribution, we provide a thorough taxonomic description of *Psyllaephagus migrator* sp. nov. complete with high-resolution images, collection data, host associations, and DNA sequences to facilitate further research. Still saddled with the questionable origin of *P. migrator* in Florida, we document attempts to compare the new species with *Psyllaephagus* specimens reared from

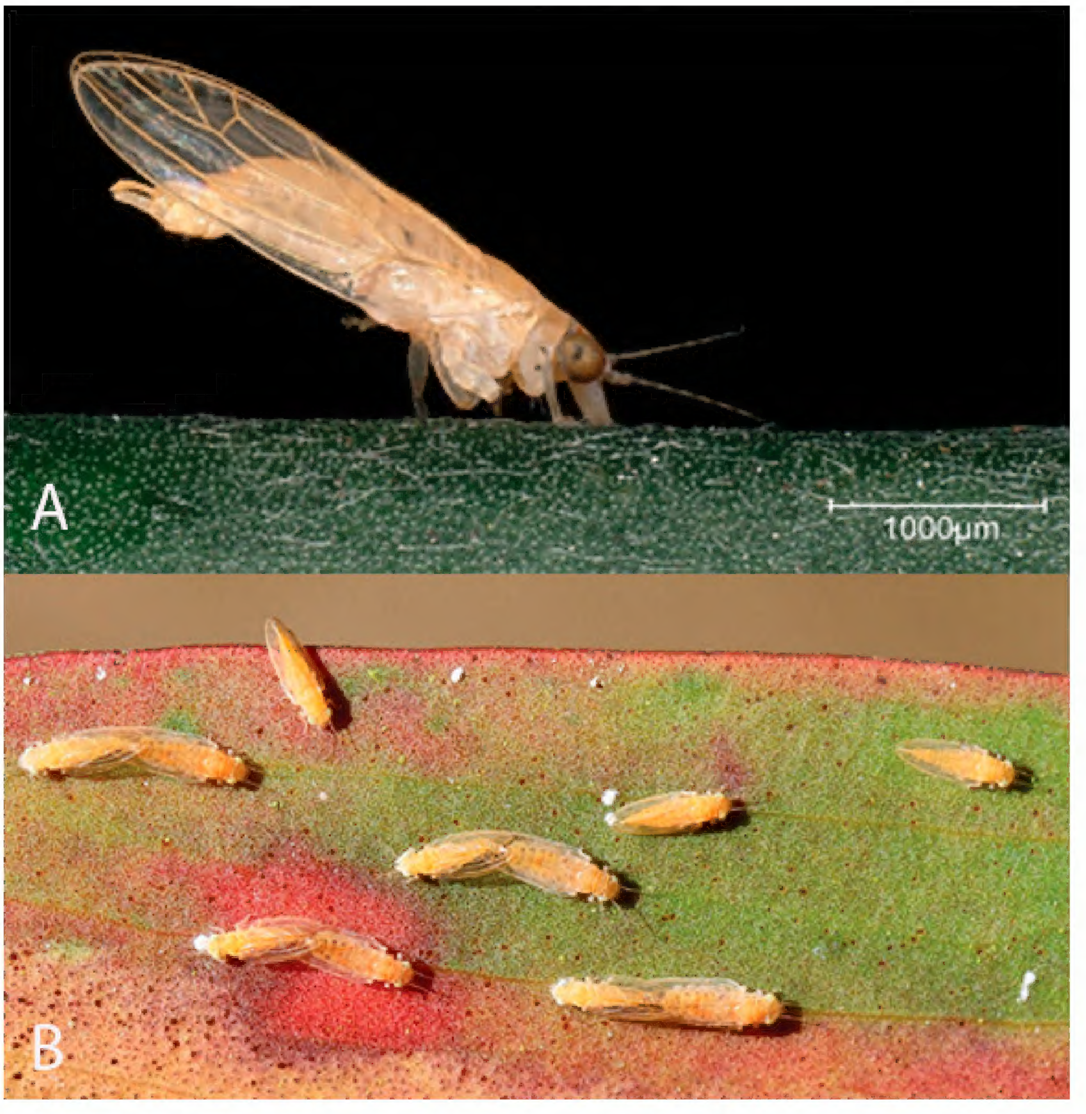

Figure 1. A *B. melaleucae* male **B** *B. melaleucae* mating pairs.

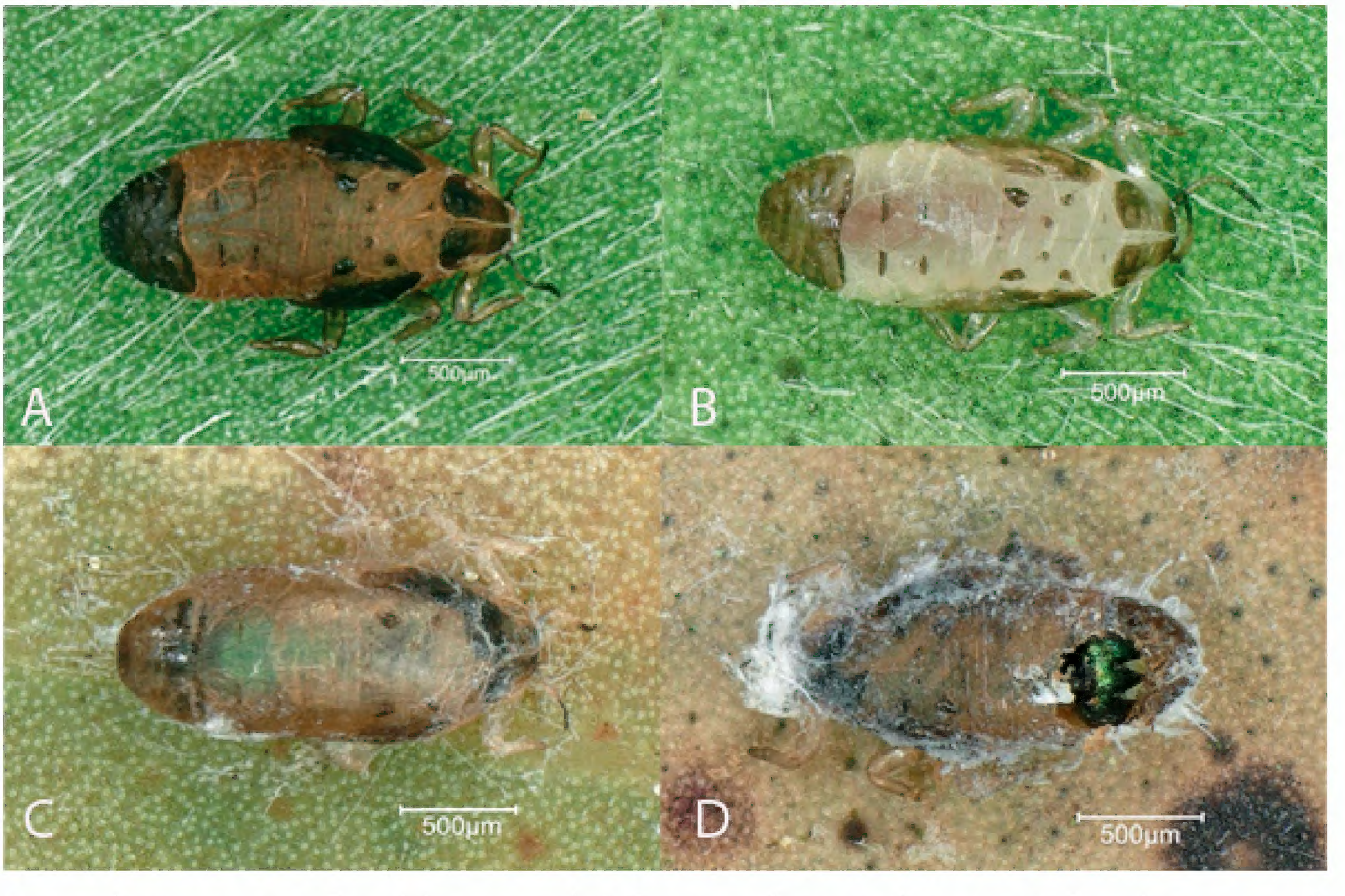

Figure 2. A parasitized *B. melaleucae* nymph **B** *P. migrator* last instar larvae inside *B. melaleucae* nymph **C** *P. migrator* just before emergence **D** *P. migrator* emerging.

B. melaleucae in Australia. Finally, we present psyllid trap data demonstrating an apparent population decline of *B. melaleucae* at a few Florida localities, first detectable in 2014. These trap data and their correlation to the presence of *P. migrator* is firmly anecdotal but correlates well with the emergence of a *B. melaleucae* parasitoid in Florida.

Materials and methods

Abbreviations used

Depositories & Institutions

FSCA	Florida State Collection of Arthropods
FDACS-DPI	Florida Department of Agriculture and Consumer Services, Division of Plant Industry
SAMA	South Australian Museum
ABCL	Australian Biological Control Laboratory
USNM	National Museum of Natural History, Washington DC
CDFA	California Department of Food and Agriculture, California
EMEC	Essig Museum of Entomology, Berkeley California
CASC	California Academy of Sciences, San Francisco California
QM	Queensland Museum, Brisbane Australia
NHMUK	Natural History Museum, London United Kingdom

Morphological terms

OOL	ocellocular line
POL	posterior ocellar line
AOL	anterior ocellar line
F1-F6	Funicle segments 1 through 6
MV	marginal and submarginal veins combined
PMV	postmarginal vein
STV	stigmal vein

Psyllaephagus collections

On April 9, 2020, a single leaf of *M. quinquenervia* containing two parasitized *B. melaleucae* nymphs was collected from a small patch of melaleuca trees located in Port St. Lucie, St. Lucie County, Florida. The leaf was placed in a small storage container until the parasitoids emerged. The adult *Psyllaephagus* were placed in 70% ethanol. Subsequent collections were made in April 2021, 2022, and 2023. Specimens were deposited at FSCA, the South Australia Museum (SAMA, Adelaide, Australia) and the Queensland Museum (QM, Brisbane, Australia). Australian specimens were

reared from parasitized *B. melaleucae* collected from *M. quinquenervia* leaves in Peregian Environmental Park (Queensland, Australia) on July 5, 2023. Adults were placed in 95% ethanol. Two male and two female specimens from this rearing event have been deposited at the Queensland Museum (QM, Brisbane, Australia) (Suppl. material 1).

Specimen photography

Images at FSCA were produced with a Macropod microphotography system using 10× and 20× Mitutoyo objective lenses and were rendered in Helicon focus. Images of molecular voucher specimens are deposited in BOLD (Barcode of Life Database), in association with their sequence and collection data (Suppl. material 2). Images for 1A,2,3,8 were produced with a Keyence VHX-5000 Digital Microscope using live specimens. Fig. 1B was taken with a Canon EOS 7D fitted with a 100 mm macro lens with natural light. Additional images (Fig. 5A–E, H) were produced with a Leica M205C stereo microscope with a KS5 camera.

Psyllaephagus morphological identification

Male and female *Psyllaephagus* sp. were subjected to the available identification keys for Australia, New Zealand, southern Africa, India, China, the Palearctic Realm, Costa Rica, and California (Riek 1962; Prinsloo 1981; Noyes 1988; Trjapitzin 1989; Noyes and Hanson 1996; Singh 1996; Zuparko 2019; Wu et al. 2021; Noyes 2022; Noyes 2023). The next identification strategy involved generating a list of all valid *Psyllaephagus* species from Noyes (2019). The taxa in this list were then eliminated as possible identifications for the Florida *Psyllaephagus* specimens based on 1) their inclusion in previously mentioned dichotomous keys or 2) comparison to original descriptions and illustrations for species not included in older keys. The Zoological Record™ on Web of Science was queried for *Psyllaephagus* taxonomic literature that was unaccounted for in Noyes (2019).

McClelland et al. (2023) posited that if *Psyllaephagus* species cannot be diagnosed against the type material of A. A. Girault, the default assumption should be that they are not conspecific. That approach is adopted here. The combination of taxonomic description, accurate host and locality data, high resolution images, and DNA sequence data presented here provides a robust toolkit for future identifications and taxonomic research on *Psyllaephagus*.

DNA extraction, PCR, and sequencing

DNA extraction and PCR amplification were performed at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry (FDACS-DPI) for Florida specimens and Australian specimens were processed at the Australian Biological Control Laboratory (ABCL). Newly generated sequences were deposited in GenBank (Accession numbers: PP831165–PP831171 COI; PP833155–PP833161 18S; PP837610–PP837615 28S; PP840063–PP840065 CytB; PP840067–PP840074 ITS2) and BOLD

(PMIG001-24; PMIG002-24; PMIG003-24; PSYMI001-24; PMIG005-24; PMIG006-24) (Suppl. material 2). Sequence chromatograms were trimmed and assembled into contigs in Geneious Prime® 2023.2.1 (FDCAS-DPI) or 2021.2.2 (ABCL). Sequences were manually checked to ensure that there was no evidence for the presence of pseudogenes.

At FDACS-DPI, genomic DNA was nondestructively extracted using the Qiagen DNeasy Kit (Taekul et al. 2014; Sabbatini Peverieri et al. 2018). PCRs were set up as 25 µL reactions using the Kapa HiFi HotStart Ready Mix Kit per the manufacturer's recommended protocol (Tables 1, 2). Three µL of genomic DNA extract were used per PCR. Positive PCRs were purified with the Qiagen QIAquick PCR Purification Kit. Purified amplicons were sequenced bidirectionally on the ABI SeqStudio platform with ABI BigDye Terminator v.3.1 Cycle Sequencing Kit chemistry.

At ABCL, genomic DNA was nondestructively extracted by incubating specimens in 20 µL of QuickExtract solution (LGC Biosearch Technologies, Middlesex, UK) for 20 mins at 65 °C, then 98 °C for 2 mins. PCR reactions used MyTaq™ HS DNA Polymerase (Meridian Bioscience, Ohio, USA) as per the manufacturer's recommended protocol and using the primers and PCR conditions on Tables 1, 2 respectively. Each reaction used 2 µL of genomic DNA extract and a 12 µL total reaction volume. Positive PCRs were purified enzymatically by adding 1 U each of Exonuclease I and Antarctic Phosphatase (New England Biolabs, Massachusetts, USA) to the PCR products and incubating at 37 °C then 80 °C, each for 15 mins, before sequencing for 15 mins. Purified amplicons were sequenced bidirectionally on a ABI3730XL at Macrogen (South Korea).

Psyllaephagus molecular identification

Sequence data for five gene regions (18S, 28S, ITS2, CytB, COI) (Suppl. material 2) were queried to the NCBI GenBank (National Center for Biotechnology Information 1988) nucleotide database and *Psyllaephagus* Sequence Read Archives (SRAs with 1000 max targets returned) by MegaBLAST (Morgulis et al. 2008) and BLASTn searches (Altschul et al. 1990). COI sequences were queried to the BOLD (Ratnasingham and Hebert 2007) Animal Identification Engine with the "All Barcode Records on BOLD" setting. New sequences were also compared to unpublished data for *Psyllaephagus* from Australia and Réunion (pers. comm. McClelland and Gomard 2023). Sequences from Florida and Australian populations were aligned using the default settings of MUSCLE (Edgar et al. 2004) as implemented in MEGA7 (Kumar et al. 2016). Alignments were manually trimmed to ensure complete data coverage for comparison. Variance between these populations was calculated using p-distance.

Suction trap survey

The FDACS_DPI, along with several collaborators, maintains suction traps in Florida. These are large machines that operate continually and sample the air for flying insects (Halbert and Burckhardt 2020). Short traps are 2 m tall, and tall traps are 8 meters. Three tall traps, in Miami, Immokalee, and Winter Haven, began operating prior to the

Table 1. PCR and Sanger sequencing primers used in this study.

Region/Primer	Sequence (5'-3')	Citation
18S		
18S-H17F	AAATTACCCACTCCCGGCA	Heraty et al. (2004)
18S-H35R	TGGTGAGGTTTCCCGTGTT	Heraty et al. (2004)
18S-2880	CTGGTTGATCCTGCCAGTAG	Tautz et al. (1988)
18S-B	CCGCGGCTGCTGGCACCAGA	von Dohlen and Moran (1995)
28S		
28S-D23F	GAGAGTTCAAGAGTACGTG	Park and Foighil (2000)
28S-b	TCGGAAGGAACCAGCTACTA	Whiting et al. (1997)
ITS2		
Forward 5.8S	GGCTCGTGGAATCGATGAAGAACG	Pilgrim and Pitts (2006)
Reverse 28S	GCTTATTAATATGCTTAAATTCAGCGG	Weekers et al. (2001)
CytB		
CB2	ATTACACCTCCTAATTTATTAGGAAT	Jermiin and Crozier (1994)
CP1	GATGATGAAATTGGATC	Harry et al. (1998)
COI		
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)

Table 2. PCR thermocycler conditions.

Primer Pair	Thermocycler conditions
18S-H17F/18S-H35R	1) 98C/3 min; 35× of steps 2–4: 2) 95C/30 sec; 3) 52C/45 sec; 4) 72C/1 min; 5) 72C/10 min; 4C/∞
18S-2880/18S-B	1) 98C/3 min; 35× of steps 2–4: 2) 95C/30 sec; 3) 59C/45 sec; 4) 72C/45 sec; 5) 72C/10 min; 4C/∞
28S-D23F/28S-b	1) 98C/3 min; 35× of steps 2–4: 2) 95C/30 sec; 3) 57C/45 sec; 4) 72C/1 min; 5) 72C/10 min; 4C/∞
Forward 5.8S/Reverse 28S	1) 98C/2 min; 32× of steps 2–4: 2) 98C/30 sec; 3) 60C/30 sec; 4) 72C/30 sec; 5) 72C/7 min; 4C/∞
CB2/CP1	1) 98C/2 min; 32× of steps 2–4: 2) 98C/30 sec; 3) 50C/30 sec; 4) 72C/30 sec; 5) 72C/7 min; 4C/∞
LCO1490/HCO2198	1) 98C/3 min; 32× of steps 2–4: 2) 95C/30 sec; 3) 50C/30 sec; 4) 72C/45 sec; 5) 72C/7 min; 4C/∞

initial release of *B. melaleucae* in April, 2002. Short traps in Immokalee were installed between 2007 and 2011, and a short trap in Winter Haven was installed in 2005. Specimens of *B. melaleucae* were counted and recorded from each weekly sample. To obtain yearly values for Immokalee short traps, yearly catches were totaled for all the traps that ran for most of the year, and that sum was divided by the number of operating traps.

Results

Psyllaephagus morphological identification

None of the available identification keys resulted in a morphological match for the Florida *Psyllaephagus*. Couplet functionality generally broke down in the early steps of the identification keys. Drawn from Noyes (2019) and subsequent taxonomic literature, 250 valid *Psyllaephagus* species were eliminated as identification matches for the Florida specimens. A total of at least 20 undescribed species, from North America (Zuparko 2019) and an additional 20 from Australia (ARM, personal observation) were also eliminated as possible identifications (Suppl. material 3).

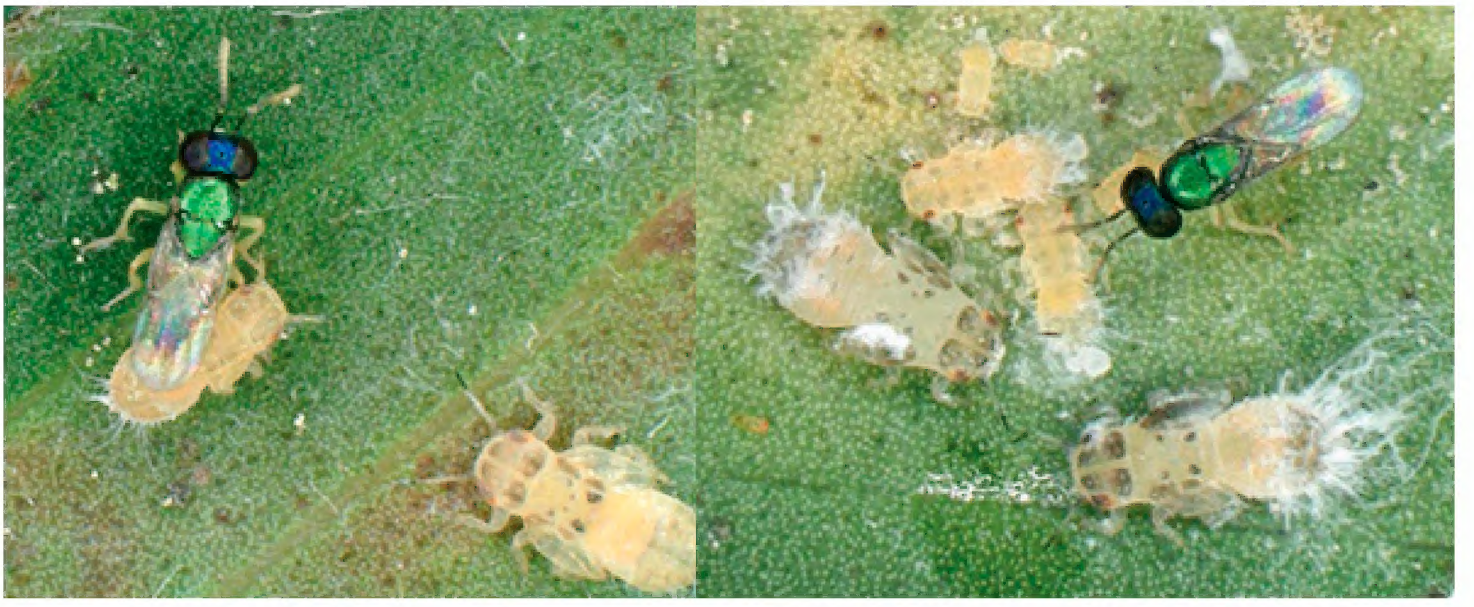

Figure 3. *P. migrator* parasitizing a nymph of *B. melaleuca* (L) and palpating (R).

There was one reference to a *Psyllaephagus* species emerging from *B. melaleucae* in its native Australia (Purcell et al. 1997). Specimens of this *Psyllaephagus* were sent to the Queensland Museum for identification (Purcell et al. 1997). However, these specimens were not accessioned into the Queensland Museum collection and appear to be lost. It is likely that they were not identified confidently to genus at the time (pers. comm Burwell C, June 2023). Evidence of the host association between *Psyllaephagus* and its psyllid host were confirmed during the collection events in Florida and Australia, which confirmed that *Psyllaephagus* does parasitize *B. melaleucae* (Figs 2, 3).

Psyllaephagus molecular identification

The COI gene forward primer, LCO1490, produced poor quality traces for Australian specimens. The ITS2 region contained two homopolymer repeats that resulted in low quality base calls for some Florida and Australian specimens. Sequence queries to the GenBank nucleotide database yielded no significant matches above 96.3% similarity. The highest BLAST sequence similarity for coding gene fragments ranged from 83.3% (CytB, to *Psyllaephagus* sp.) to 96.3% (18S, to *Trichospilus* sp. D2108). The top COI sequence similarity in BOLD was an 87% match to an unidentified Thai encyrtid (BIN BOLD:AFE5495). The top twenty matches in BOLD were all Encyrtidae sequences ranging from 84.8% to 87.0% similarity. BLAST searches of three *Psyllaephagus* SRAs (SRX17783156; SRX19171555; SRX19171556) yielded no significant matches other than 18S. Ribosomal sequence data (18S, 28S, ITS2: 1,594 bp positions) were highly similar between Floridian and Australian samples; only a single ITS2 polymorphism was detected in an Australian specimen. Mitochondrial sequence data (COI, CytB) were much more variable. COI sequences from Florida varied by 3.5% to 3.7% compared to Australian samples (545 bp positions). CytB sequences from Florida varied by 1.1% to 4.0% compared to Australian samples (175 bp positions). No amino acid sequence variation was detected among these mitochondrial targets.

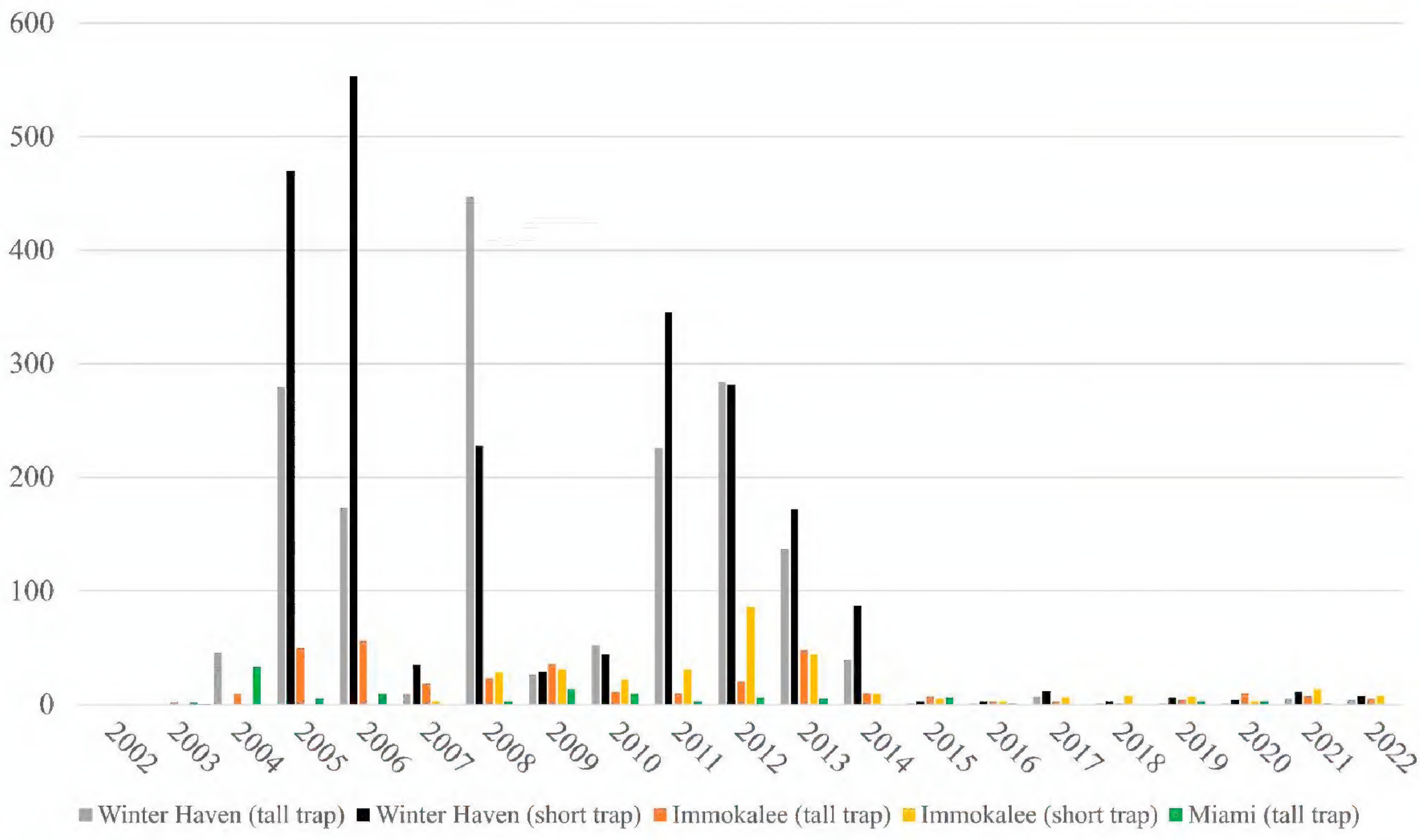

Figure 4. Suction trap collections of *Boreioglycaspis melaleucae* (Moore) at three locations in peninsular Florida, Winter Haven, Immokalee, and Miami beginning in 2002, when *Boreioglycaspis melaleucae* (Moore) was released initially. Tall traps are 8 m tall, and short ones are 2 m. All three tall traps operated the whole time. The short trap in Winter Haven was installed in February 2005. Five short traps in Immokalee operated for various intervals between 2007 and 2022. To obtain values for Immokalee short traps, yearly catches were totaled for all the traps that ran for most of the year, and that sum was divided by the number of operating traps.

Suction trap survey

Yearly tallies show a marked decline in numbers of *B. melaleucae* beginning in 2013 and progressing to insignificant catches by 2015 in all traps (Fig. 4). As expected with data on species colonizing a new environment, populations fluctuated enormously after an initial peak shortly after colonization. It is unclear why numbers declined so severely after 2013.

Tall traps in Miami and Immokalee collected two specimens each in the year following the initial release of *B. melaleucae*. Specimens were collected in the tall trap in Winter Haven about two years after release, a distance of about 240 km from the main release site.

Taxonomy

Terminology for adult body morphology follows Riek (1962), Noyes (1984), Gibson (1989), the Hymenoptera Anatomy Ontology portal (Yoder, Mikó, Seltmann, Bertone, Deans 2010). Size variation amongst the type series was not discernible so measurements were only taken from the female holotype and male allotype. While some minor biological variation is naturally expected, no exceptional differences were found during examination of the type series. Specimens were examined using a Leica M205C stereo microscope.

Genus *Psyllaephagus* Ashmead, 1900

Type species. *Encyrtus pachypsyllae* Howard, 1885, by original designation (U.S Dept. Agr. Bur. Ent. Bull. No.5, 15). For generic synonymy see Noyes (1984) and Dahms (1997).

Note. *Psyllaephagus migrator* sp. nov. clearly belongs in the genus *Psyllaephagus* based on the key to genera in Noyes (1984), characterized by the following characters: brightly metallic green, blue-green or copper colour; punctiform marginal vein of the fore wing which is not more than twice as long as broad; fore wing with stigmal vein longer than postmarginal vein; mandibles with one or two teeth and a truncation; a hypopygium that does not extend more than two-thirds along the gaster.

Psyllaephagus migrator McClelland, sp. nov.

https://zoobank.org/31BFCF40-024E-4442-AED4-5FAEB0312865

Figs 5–7

Material examined. ***Holotype.*** USA • Female (FSCA): "USA – Florida, St. Lucie Co., Port St., Lucie. Peacock Run Apartments. 27.3462297N, 80.3827508W. 17THApril 2023; M. Hentz; reared from parasitized nymphs of *Boreioglycaspis melaleucae*". Genbank accession numbers: PP840072; PP837614; PP833159; PP831170; PP840063. BOLD: PMIG006-24 Specimen deposited at FSCA, accession number: FSCA 00094033.

Allotype. USA • Male (FSCA): Collection data as for holotype. Genbank accession numbers: PP840071; PP837613; PP833160; PP831169; PP840064. BOLD: PMIG005-24. Specimen deposited at FSCA, accession number: FSCA 00094034.

***Paratypes*:** Collection data as for holotype, 32 females, 31 males deposited as follows: QM 7 female, 12 male; FSCA 18 female, 13 male; USNM 2 female, 1 male; CDFA 1 female, 1 male; EMEC 1 female, 1 male: CASC 1 female, 1 male; NHMUK 2 female, 2 male.

Additional material. USA • 3 Female, 2 male, point mounted: "USA- Florida, St. Lucie Co., Port St. Lucie, 5532 NW E. Torino PKWY 27.34557N, -80.37937W. 8th April 2023; M. Hentz". QM accession numbers: T260235-T260239.

AUST • 2 Female, 2 male, 1 unspecified, point mounted: AUST – "Qld, Peregian Environmental Park, 5th July 2023. Reared from parasitized *B. melaleucae* collected from *M. quinquenervia* leaves". QM accession numbers: T260240-T260244.

See Suppl. material 1 for repository accession numbers, and Suppl. material 2 for sequence data and Genbank and BOLD accession numbers of paratypes and additional material.

Diagnosis. *Psyllaephagus migrator* is a small species with purple head, blue mesoscutum, axilla and scutellum; axilla is smooth by comparison to the mesoscutum and scutellum; blue propodeum with long pale hairs on the lateral surfaces. Dark green mesopleuron and metasoma with coppery reflections. Reticulated sculpturing, reticulate-rugulose on the mesoscutum, scutellum and head.

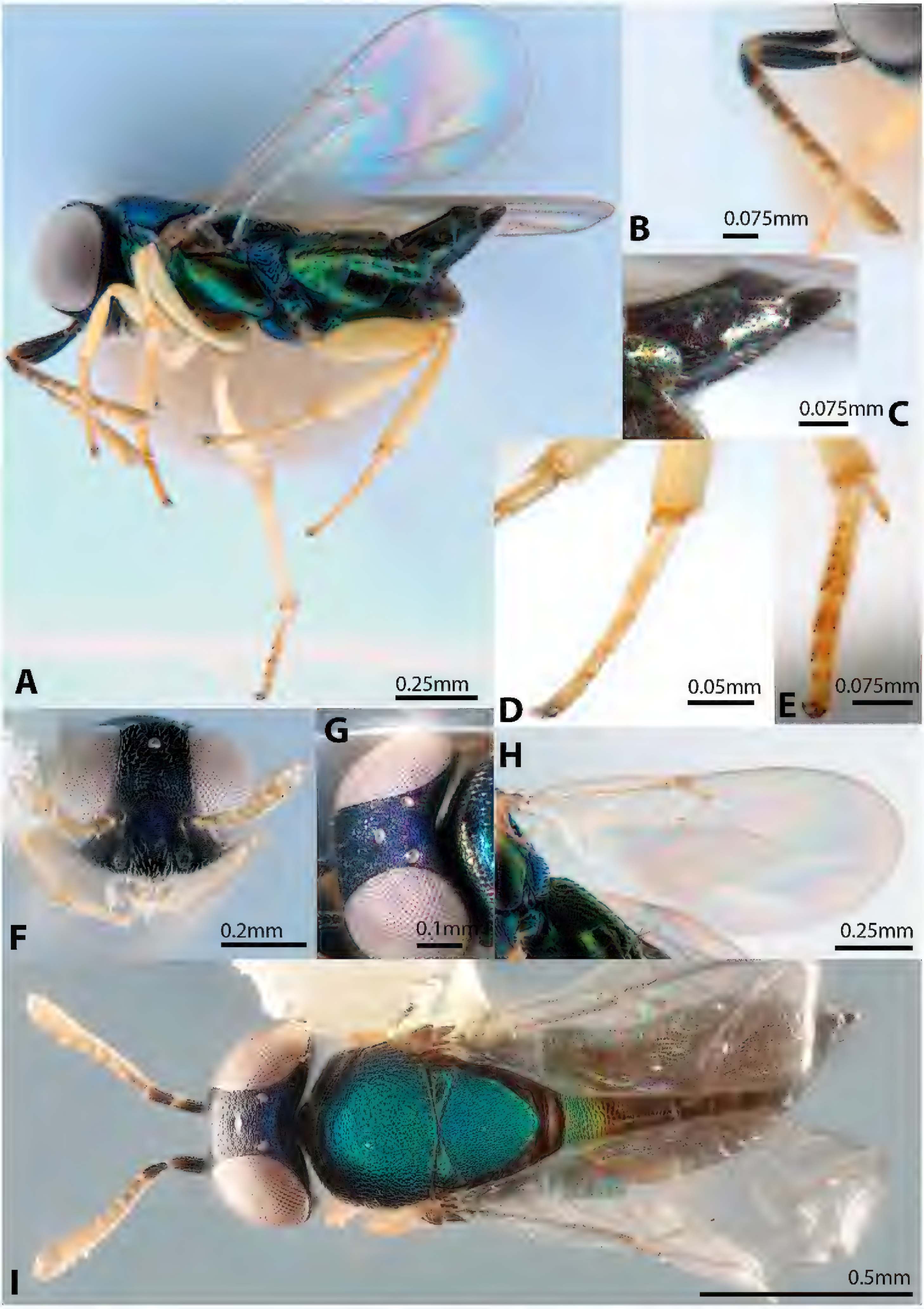

Figure 5. Female *Psyllaephagus migrator* sp. nov. **A** lateral habitus **B** scape and antennae **C** ovipositor **D** hind tibia showing fringe of setae at base and tarsus **E** mid-leg tarsus showing unique rows of pegs **F** face **G** ocelli and head color **H** fore wing **I** dorsal habitus.

A key to 60 of the 122 Australian *Psyllaephagus* fauna was published by Riek (1962). When assessing the female holotype of *P. migrator* against this key, the key terminates at couplet 43 (44) *P. discretus*. *Psyllaephagus migrator* differs from *P. discretus* in head, club and coxal color. Specifically, in the description for *P. discretu*s the head color is described as green, antennal club slightly darkened, mesocoxa slightly darkened at base and metacoxal dark. *Psyllaephagus migrator* has a purple head with blue reflections, light brownantennal club, and all coxae are yellow..

The Australian species that are not included in Riek's key have been morphologically examined and were eliminated. Specifically, the three species described by Walker (1839) all have a significant space between the posterior ocelli and the eye margin, whereas *Psyllaephagus migrator* has a marginal space. The key morphological differences separating the new species from the other described Australian species, *P. iridus*, are leg color (yellow in *P. migrator* versus dark brown/bi-colour in *P. iridis*) and peg pattern on the basitarsus (two sharply angled opposing rows of pegs in *P. migrator* versus one continuous row of pegs in *P. iridus*). Males of *P. iridu*s also have very distinct yellow-ended, capitate antennae. As in McClelland et al. (2023), *Psyllaephagus migrator* is not diagnosed against the Australian species described by Girault due to the morphologically uninformative state of his type specimens.

Psyllaephagus migrator was diagnosed against the valid North American species (Suppl. material 3) and superficially resembles *P. pachypsyllae*, known only from North America (Noyes, 2023). *P. migrator* differs from *P. pachypsyllae* in the characteristics of the tegula. The tegula base in *P. migrator* is dark brown in females, light brown in males. The tegula in *P. pachypsyllae* is pale yellow at the base.

Description. Females can be identified by the following combination of characters: prepectus dark brown anteriorly with white posterior edge; tegula light brown, sometimes with darker brown patches; legs pale yellow, apical segments with dark brown tips; mesotarsus with distinct row of orange pegs on underside; mesotibial spur stout; base of metatibia fringed with stout orange hairs; ovipositor slightly extruded; three very long cercal hairs; dark brown scape; space between posterior ocelli and eye margin less than a quarter diameter of ocelli; distance between posterior ocelli slightly greater than distance between posterior and anterior ocelli; pedicel and first two funicle segments dark brown, remaining segments light brown flagellum clavate with fine, pale setae and slight but discernible space between funicle segments.

Males smaller than females, with green reflections (where females are blue) and with reticulate sculpturing as in females. Additionally, the following characters can be used to identify males of *Psyllaephagus migrator*: Prepectus dark brown anteriorly with white posterior edge, tegula light brown, sometimes with darker brown patches; legs pale yellow, tarsomeres light brown; tarsal characters as for females; space between posterior ocelli and eye margin approximately one third diameter of ocelli; distance between posterior ocelli almost twice distance between posterior and anterior ocelli; scape yellow pedicel dark brown; antenna serrate, light brown, with short pale setae; small but distinct space between funicle segments.

All measurements are in millimeters.

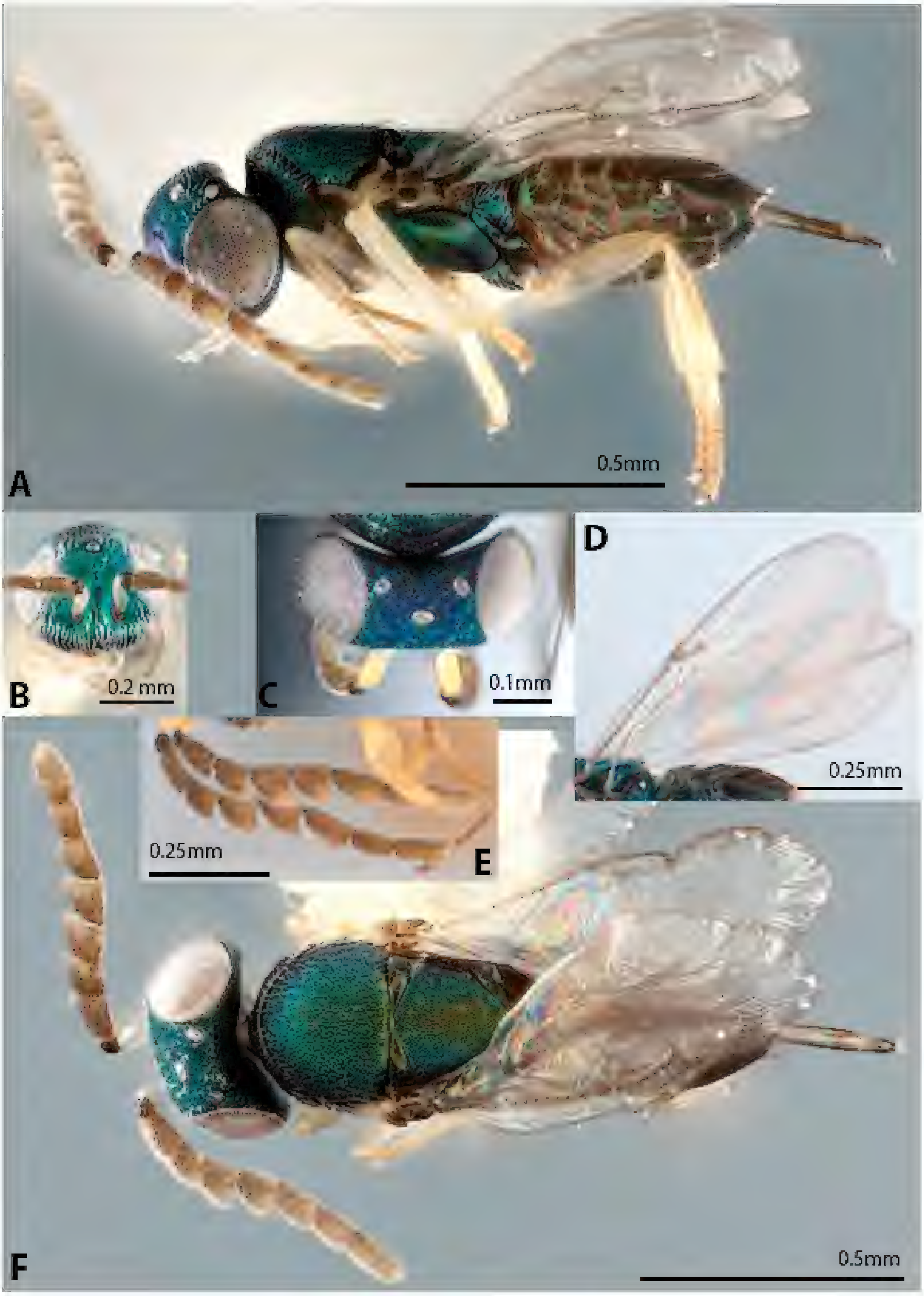

Figure 6. Male *Psyllaephagus migrator* sp. nov. **A** lateral habitus **B** face **C** head showing ocelli and scape **D** wing **E** antennae **F** dorsal habitus.

Female. ***Body.*** Length excluding ovipositor 1.53. Body blue except for mesopleuron, metasoma and gaster which are green with copper reflections (Fig. 5A, I). Reticulate sculpture, smoother on axilla and gaster, reticulate-rugulose on rest of mesosoma (Fig. 5I). Ovipositor mildly extruded, approximately 1.2× the length of

mid tibial spur (Fig. 5C, E) length 0.09 (Fig. 5C). Thorax covered with sparse, evenly distributed, short coarse setae (mesopleuron smooth); pronotum length:width 0.03:0.54, mesoscutum length:width 0.32:0.49. Tegula and prepectus dark brown, prepectus extends to tegula (Fig. 7). Legs pale yellow, apical tarsal segments with dark brown tips (Fig. 5A). Mesotarsus with two distinct angled rows of orange pegs on underside (Fig. 5E); length 0.13; apical tarsal segment 0.09. Metatibia fringed with setae,increasing in length to form a point (Fig. 5E). Gaster with coppery reflections, cercal plate pronounced, long cercal setae approximately 1/3 the length of gaster (Fig. 7). Gaster length 0.72; width 0.33. Fore and hind wings hyaline with short setae almost uniformly distributed (except for linea calva and naked basal area of fore wing) (Fig. 5H). Fore wing length 1.28; hind wing length 0.82; fore wing MV length .53; fore wing PMV length 0.03; fore wing STV length 0.09.

Head. Length excluding mandibles 0.42; width (frontal view) 0.55; depth (lateral view) 0.28. Head purple with blue reflections, dense reticulate sculpturing, sparse setae (Fig. 5F, G). Mandible pale, almost white (Fig. 5F). Posterior ocelli with small distance between them and eye margin (Fig. 5G). POL 0.1; AOL 0.07; OOL 0.007. Malar space 0.12. Eye length 0.33; width 0.26. Scape mildly expanded on underside, narrowest at base; dark brown with pale tip below pedicel; carination not obvious (Fig. 5B); length 0.2. Pedicel dark brown in the basal ¾, paler brown at apex; length 0.08; width 0.03. Antenna clavate, light brown; uniform setae on each funicle; minimal distance between funicle segments 0.004 (Fig. 5B). Funicle length:width; F1 0.05:0.03; F2 0.04:0.03; F3 0.05:0.03; F4 0.05:0.03; F5 0.04:0.04; F6 0.05:0.04. Club length 0.13; width 0.06.

Male. ***Body***. Length 1.01. Body green with blue reflections on head and thorax, copper reflections on gaster (Fig. 6). Sculpture reticulate, smoother on axilla and gaster, reticulate-rugulose on rest of mesosoma, pronotum and mesoscutum with uniform, pale setae (Fig. 6A, F); pronotum (length:width) 0.04:0.32; mesoscutum (length:width) 0.24:0.36. Prepectus dark brown anteriorly with white posterior edge, tegula light brown, sometimes with darker brown patches (Fig. 6A). Legs pale yellow with light brown tarsomeres, basitarsus length 0.07; apical tarsal segment 0.07 (Fig. 6A). Gaster dark green with copper and blue reflections (Fig. 6A) (length:width) 0.38:0.22. Fore and hind wings hyaline with short setae almost uniformly distributed (except for linea calva and basal area of the fore wing) (Fig. 6D). Fore wing length 0.93; hind wing length 0.6; fore wing MV length 0.34; fore wing PMV length 0.07; fore wing STV length 0.08.

Head. Length excluding mandibles 0.35; width (frontal) 0.41; depth (lateral view) 0.19. Reticulate sculpturing with short, pale setae uniformly covering head. Head dark green with blue reflections, becoming emerald as reticulation smooths and setae become sparser on the face (Fig. 6B). Mandible very light brown. Posterior ocelli at a distance of approximately 1/3 of their diameter from the eye margin (Fig. 6C). POL 0.11; AOL 0.06; OOL 0.012. Malar space (0.12; 0.13; 0.13, see comments below). Eye length 0.23; eye width 0.19. Scape mildly expanded on underside, narrowing towards base, yellow, carination not obvious, covered in pale setae (Fig. 6B, C); length

0.09. Pedicel uniformly dark brown; length 0.05; width 0.04. Antenna serrate, light brown, shaft light brown; dense, uniform pale setae on each funicle (Fig. 6E); distance between segments 0.006. Flagellomere length:width; F1 0.08:0.04; F2 0.07:0.06; F3 0.08:0.08; F4 0.08:0.07; F5 0.11:0.06; F6 0.09:0.04.

Host. *Boreioglycaspis melaleucae* Moore

Distribution. Currently only known from the type locality in Florida, USA and southeastern Queensland, Australia. However, the species is likely to be more broadly distributed given that its host psyllid, *Boreioglycaspis melaleucae*, has spread to all 22 central and southern Florida counties, and has been collected and recorded from all Australian states and territories except South Australia (Burkhardt 1991). The psyllid's host plant, *Melaleuca quinquenervia* is a widespread invasive plant in Florida and is recorded from coastal regions of all Australian states and territories.

Figure 7. Lateral habitus of female *Psyllaephagus migrator* sp. nov. showing detail of prepectus and tegula (circled left) and cercal setae (circled right).

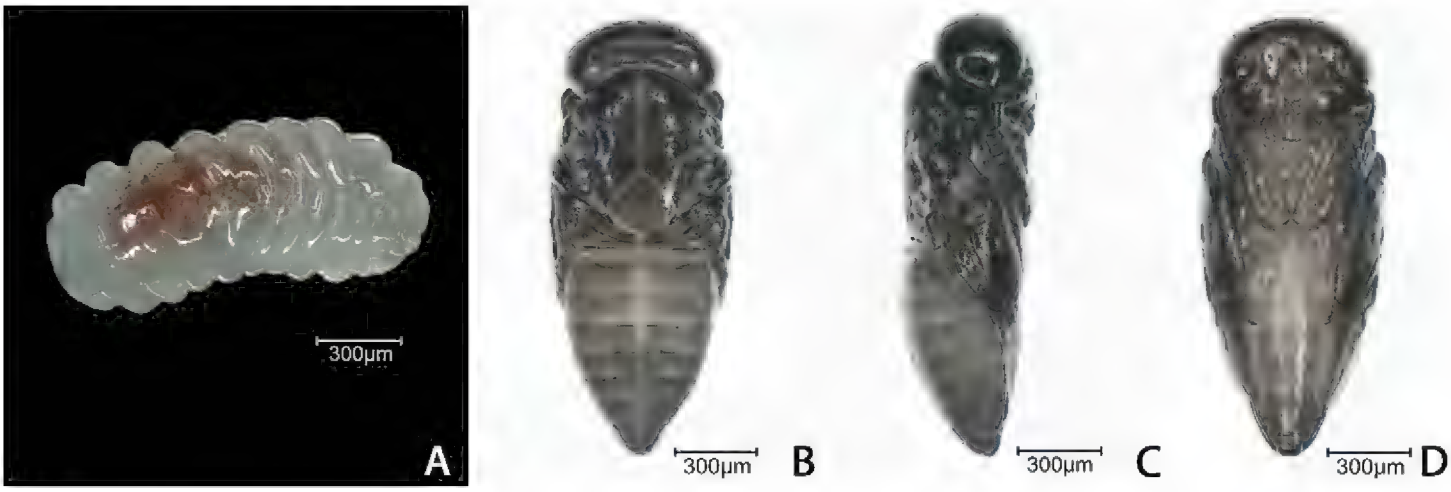

Figure 8. Juvenile stages of *Psyllaephagus migrator* **A** final instar larva **B** pupa dorsal **C** pupa lateral **D** pupa ventral.

Etymology. The species epithet, *migrator*, meaning wanderer or immigrant in Latin and references the vast distance between the locations where the species has been collected.

Comments. The malar space on the male allotype is partially obscured and so the measurement given is taken from three other males in the type series. In females, it is difficult to accurately measure the ovipositor without dissecting and slide mounting the specimen and so the decision is made to measure the extrusion of both sheath and stylets past the terminal end of the outer ovipositor plate, in lateral view. In both sexes, the pronotum is difficult to measure as it curves markedly and is very small. The length is taken at the midpoint of the pronotum, dorsally, with the body not tilted.

Although not exclusively suitable for morphological diagnosis, we also present images of the immature stages of *P. migrator* (Fig. 8) completing a set of high-resolution biological and diagnostic images from host to adult.

Discussion

Our observations constitute the first confirmed record of *Boreioglycaspsis* as a host of *Psyllaephagus* wasps, with the association found in Florida and Australia. *Psyllaephagus migrator* is currently known from only a few Florida counties and southeastern Queensland. However, *B. melaleucae* has a broad distribution in Australia (Burckhardt 1991) and its host tree *M. quinquenervia* is native to Australia and Melanesia (GBIF 2024). This tritrophic tree-psyllid-wasp system could conceivably occur across a large biogeographic area. Thus, the precise source of this new adventive species in Florida is unresolved, especially given the lack of an Australian haplotype match. How *P. migrator* arrived in Florida remains a mystery, but there are some intriguing leads worth discussing.

In 2006 and 2009, *B. melaleucae* was discovered on *M. quinquenervia* trees near San Juan, Puerto Rico and in Los Angeles County, California, respectively (Pratt and Arakelian 2011; Pratt and Center 2012). Both unintended introductions of *B. melaleucae* were documented after the approved release of the psyllid in Florida during the spring of 2002 (Center et al. 2006), leading to the conclusion that Florida was the most likely source population based on winged-dispersal versus anthropogenic models (Pratt and Center 2012). Unfortunately, mitochondrial data did not distinguish California and Florida *B. melaleucae* from Australian populations (Pratt et al. 2013) and thus were not useful to test this hypothesis.

Approximately 140 encyrtids have been introduced into United States territory, and about 80 of these occur on the mainland, excluding Alaska and Hawaii (Simpson et al. 2021). Several adventive *Psyllaephagus* have now established in the continental United States, and only *P. bliteus* Riek was intentionally introduced as a biological control agent (Paine et al. 2000). Interestingly, *P. parvus* Riek and *P. perplexus* Riek, both Australian species, were discovered in California in analogous cases of unintended introduction during 2007 (Eatough Jones et al. 2011). The arrival of non-native parasitoids, attacking non-native hosts on a distant continent, is not in itself surprising. A recent analysis of parasitoid movement between continents found that the phenomenon

is somewhat common, albeit for a different superfamily of parasitoid wasps (Moore et al. 2023). The biological details of parasitoids and their host are the crucial determinants that incline some species to human mediated dispersal. For endoparasitoids of cryptic hosts, such as eggs or life stages inside plant tissue, long distance movement via trade of plant material is not difficult to envision. The only known host of *P. migrator*, *B. melaleucae*, is an external feeder on live trees and does not form galls; this essentially precludes the possibility of transport on dead plant material. Thus, *P. migrator* could have likely been transported to Florida within parasitized *B. melaleucae* nymphs hosting on *M. quinquenervia* or a close relative (see Purcell et al. 1997).

We can be certain that the introduction occurred by 2020 when the first specimens were discovered. However, the precipitous decline of adult *B. melaleucae*, as indicated by trap numbers, began around 2013 and has continued to the present. These trap numbers and the presence of a new parasitoid make for an interesting correlation, although we cannot directly assess causality. Indeed, classical biological control agent populations are expected to fluctuate (e.g., see Zalucki and van Klinken 2006) and it now seems unlikely that *B. melaleucae* numbers will dramatically increase again in Florida without augmentation or local extinction of *P. migrator*. *Psyllaephagus migrator* has not been encountered in California (Robert Zuparko, pers. comm. August 2023), but it is suspected that at least one other unidentified *Psyllaephagus* species in California is an Australian adventive (Zuparko 2019). No information from Puerto Rico is available, and surveying there for *B. melaleucae* and parasitoids is a logical next step. Alternatively, *P. migrator* could have been in Florida since 2002 when *B. melaleucae* was deliberately released as a classical biological control agent of *M. quinquenervia*. However, there are no specimens to suggest this. Furthermore, this would assume that the original quarantine colony of *B. melaleucae* harbored these parasitoids and the parasitoids were not noticed. That seems highly unlikely and it is reasonable to exclude this as a possible source of *P. migrator* in Florida.

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Supplementary material 1

Sequence data and associated accession numbers

Authors: Matthew R. Moore, Matthew G. Hentz, Virgine T. Singarayan, Bradley T. Brown, Dean R. Brooks, Alana R. McClelland

Data type: docx

Link: https://doi.org/10.3897/jhr.98.133593.suppl1

Supplementary material 2

Table of the speciemens deposited, where they were deposited, sex, type and collection data

Authors: Matthew R. Moore, Matthew G. Hentz, Bradley T. Brown, Alana R. McClelland

Data type: xlsx

Link: https://doi.org/10.3897/jhr.98.133593.suppl2

Supplementary material 3

Morphological exclusion of the valid species of *Psyllaephagus*

Authors: Matthew R. Moore, Matthew G. Hentz, Bradley T. Brown, Alana R. McClelland

Data type: xlsx

Explanation note: Morphological exclusion of the valid species of *Psyllaephagus* indicating species name and author, the associated key to species, and the author who performed the morphological analysis to exclude known species.

Link: https://doi.org/10.3897/jhr.98.133593.suppl3